ON THE LIFE-HISTORY OF RHIZOSTOME MEDUSAE. III. ON THE EFFECTS OF TEMPERATURE ON THE STROBILATION OF MASTIGIAS PAPUA

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The fact that water temperature has a great deal to do with the initiation of strobilation has been reported for some time. However, most of the cases known are on *Aurelia* and *Chrysaora* etc., in which the onset of strobilation is correlated with low temperature (Berrill, 1949; Thiel, 1962). Contrariwise, it is known that *Cassiopea* and *Cotylorhiza* strobilate in summer (Berrill, 1949). *Mastigias papua* belongs to this group (Uchida, 1926; Sugiura, 1963). At the same time, the present author reported an indispensability of symbiosis of zooxanthellae for strobilation (1964). But in *Mastigias papua*, too, since temperature effect on the metamorphosis is evident, the case will be described in this report.

Materials and Methods

In the present work, two sets of temperature measurements were performed. (1) By following change of the temperature of natural sea water, the temperature at which the ephyrae made the first appearance was determined. (2) In the laboratory, the efficacy of the induction of strobilation under different temperature was examined. As reported in a previous paper (Sugiura, 1964), in the scyphistomae of *Mastigias papua* which have been reared in a zooxanthella-free condition, strobilation can be induced by supplying the symbionts in the culture. Temperature effect on such an induction was studied.

For approximate regulation of temperature, rearing boxes provided with electric bulbs were used. For finer control of temperature, incubators and a constant temperature room were utilized.

Considering the necessity of illumination for maintaining a healthy condition of zooxanthellae, scyphistomae were continuously exposed to the light from a fluorescent lamp during the temperature experiments.

Results

Sea water temperature and strobilation in nature

Every year, the earliest appearance of ephyrae of *Mastigias papua* in the vicinity of the Misaki Laboratory is early summer. According to the survey of 1962, it was July 11. On July 25, abundant ephyrae, which seemed to have been released recently, were obtained (Sugiura, 1963).

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Simultaneously with these observations, temperature measurements were made on the habitat. Notwithstanding the fact that the scyphistomae of *Mastigias papua* have not been found in nature so far, it may not be unjustifiable to consider that the scyphistomae must be living on the bottom of the spot where ephyrae begin to appear, particularly because the area is very limited in the innermost part of the bay. Considering that sea water temperature to be related to strobilation must be that at the bottom of the bay, measurements were taken at 1.5–3.0 m. in depth in the bays of Aburatsubo and Moroiso. The sea water temperature during the first week of the appearance of the ephyrae turned out to be 23° C. (Table I).

However, taking into account the results of indoor experiments to be given in a following section, and also the possibility that the beginning of strobilation

Table I

Sea water temperature at the time of the first appearance of the ephyrae

July 11	July 18	July 25	July 31
23.0° C.	23.0° C.	26.5–27.0° C.	26.0–29.0° C.

in nature could be at least a week before the sighting of the ephyrae, the bottom temperature for strobilation was judged to be about 22° C.

Effects of rearing temperature for the strobilation in scyphistomae with zooxanthellae

Schyphistomae having zooxanthellae, with previous history of strobilation, were reared from late autumn of the year until the next spring in boxes kept several degrees warmer than room temperature by electric bulbs. Three grades of temperature were tested. The procedure was as follows: Test organisms were put in three boxes of the same size and although temperatures in the boxes were allowed to fluctuate with the room temperature, box A was kept about 10° C. higher constantly and B a little less higher and C still closer to the room temperature. In reality the lowest temperature in A was 19° C., in B it was 17° C. and in C about 15° C. when the room temperature was around 10° C.

When the water temperature rose with the season, initiation of strobilation first occurred in A (March 21), and a month later (April 15–24) in B in 6 dishes except one, B_7 group, while no strobilation had taken place in C by that time. Water temperature at the beginning of strobilation was 20–22° C. in both A and B.

Next is a question how the result will be, if the culturing temperature is never allowed to exceed 20° C. For this purpose, the culture C was transferred to the constant temperature room of 20° C. at the middle of April before the atmosphere reached that temperature level. This group had not strobilated at least until June 25 when B_7 did. At this point (June 25), C was further divided into two classes, one being left at 20° C. while the other was returned to room temperature. The former did not strobilate all through the summer. In the latter group, however, the first strobilation took place on August 7.

In conclusion, 20° C. seems to be just below a critical level and culturing temperature has to go beyond this threshold in order to stimulate strobilation. On the basis of the almost perfect agreement between the data obtained in nature and in the laboratory, it is possible to say that 22° C. is the lowest effective temperature for inducing strobilation. Needless to say, in zooxanthella-free scyphistomae, even much higher temperatures are quite ineffective for causing strobilation.

Temperature higher than 22° C.

For studying the effect of temperature higher than 22° C., it was unavoidable to collect individuals which have failed, for some reason or another, to react to

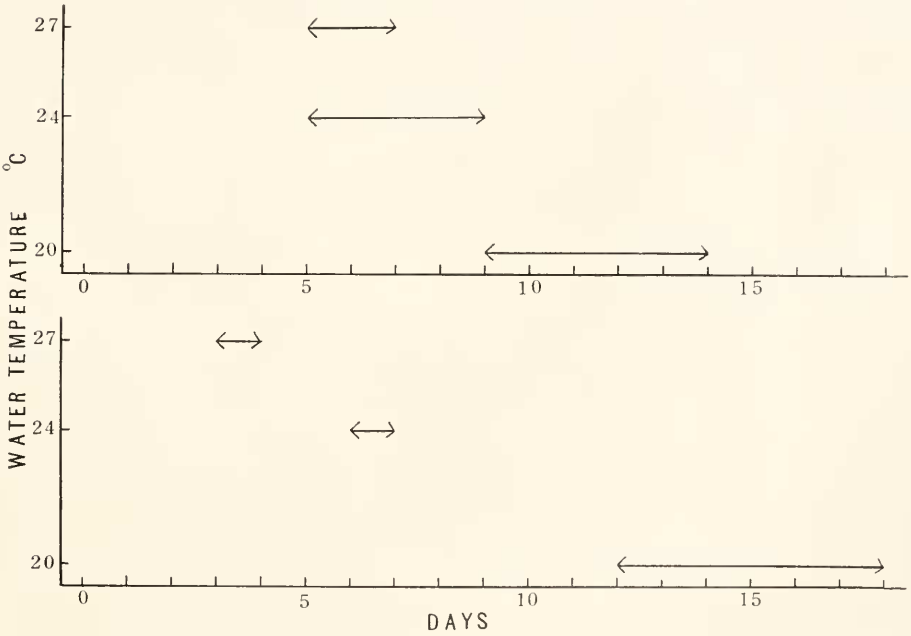

FIGURE 1. The effect of water temperature on two steps of strobilation. Upper chart: Latency between symbiosis and the beginning of morphological change for strobilation. Lower chart: Latency between the beginning of metamorphosis and the release of the ephyrae.

22° C. with strobilation. Using these organisms, a part of them (group a) was maintained at 28–29° C. for 20 days and the remainder (group b) was first set back to 20° C. for a month (Sept. 21–Oct. 21) and then to 28–29° C. In group a, no strobilation occurred in all five dishes, while among group b, strobilation began within 10 days after raising the temperature in 4 dishes out of 5.

In order to confirm the above situation further, the group a and the group b were mixed and scyphistomae were randomly divided into two parts and the two parts were equally subjected to 20° C. for a month at first (Nov. 26–Dec. 30) when one part was transferred to 25° C. and the other part kept at 20° C. In

the part made warmer, strobilation took place in all 4 dishes within a month, while in the cooler part, strobilation was seen in none of 4 dishes.

Judging from the above experiments, when scyphistomae fail once to react to 22° C., a further increase of the culturing temperature has no effect for causing stimulation. Instead, the temperature should be lowered once more for nearly a month before raising it, during which time the organisms seem to be made receptive to a warm temperature. At any rate, the main point of this finding is that it is now possible to induce strobilation by regulating the temperature, regardless of the season.

Temperature effects on separate steps of the process of strobilation

When scyphistomae which have over-wintered in a zooxanthella-free condition are given the symbionts, they strobilate immediately (within several days) with a high degree of reliability. Moreover, they can sometimes strobilate at 20° C., showing their sensitivity has been heightened by a long sojourn in a low temperature. Using such materials, the effects of 27°, 24° and 20° C. were examined concerning the latency between supplying the symbionts and the beginning of strobilation and that between the onset of strobilation and the release of ephyrae (Fig. 1). As is clear from the figure, the latter step is more sensitive to change of temperature. Since the former step mostly corresponds to the period of multiplication of symbionts, this may mean that zooxanthellae are less sensitive to temperature change than the medusa itself.

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Summary

1. In the habitat, the first appearance of the ephyrae coincides with the sea water temperature of about 22° C.

2. In the laboratory, the minimum effective range of temperature for induction of strobilation by giving zooxanthellae is found to be 20–22° C.

3. Individuals with zooxanthellae, which have once failed to react by strobilation by 20–22° C., can no longer be induced for strobilation by a further rise of temperature.

4. These individuals do react if they are cooled to 20° C. for about a month and then exposed to the higher temperature.

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